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Total-evidence analysis resolves the phylogenetic position of an enigmatic group of Paederinae rove beetles (Coleoptera: Staphylinidae)

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ABSTRACT

Paederinae is one of the most diverse subfamilies among rove beetles, yet their evolutionary history remains poorly understood. This is attributed to the limited number of phylogenetic studies, which either sought answers at a shallower taxonomic level or included limited taxon sampling. Especially problematic is the position of the rare Neotropical tribe Cylindroxystini, morphologically one of the most puzzling groups of Paederinae. The phylogenetic position of this group within Paederinae was never understood, though its rank in the classification has already been shifted twice. We assembled molecular and morphological data matrices sampled from all currently recognized Paederinae subtribes, including both genera of Cylindroxystini, and used these data to estimate phylogenetic relationships using Bayesian inference. A total of 123 morphological characters and 4,631 bp of nuclear (28S, TP, Wg, CADA, CADC, ArgK) and mitochondrial (COI) sequences were analyzed for 76 taxa. The current tribe Cylindroxystini was resolved as a monophylum within the tribe Lathrobiini as sister to the genus *Pseudolathra*, and together they are sister to the so-called ‘Medonina and allied taxa’ clade. Based on these results, we downgraded Cylindroxystini back to the subtribal level, Cylindroxystina **status reinstated,** now with a known sister group. The resulting phylogeny is the largest of the subfamily Paederinae to date and lays the foundation for establishing a natural classification of the group.

1. Introduction

Paederinae is one of the largest subfamilies of Staphylinidae, including around 7,600 species in more than 225 genera (Żyła et al., 2019; Newton A., unpublished database). The high species diversity and the limited pool of experts working on this group make Paederinae one of the most challenging rove beetle subfamilies in terms of their taxonomy and systematics. The situation is further complicated by the scarcity of phylogenetic studies targeting the group. It is clear that Paederinae remains one of the rove beetle subfamilies in dire need of a focused phylogenetic study and reclassification. Particularly noteworthy is the case of the Neotropical tribe Cylindroxystini, whose systematic position and sister-group relationships are entirely unknown.

To elucidate the current classification of the enigmatic tribe Cylindroxystini, we summarize previous phylogenetic research on Paederine and the remaining challenges, followed by a synopsis of the taxonomic history of the tribes of Paederinae. We continue with a historical overview of this tribe and the current state of knowledge on the group. Consequently, the aim of this paper is to resolve the currently unknown systematic position of the tribe Cylindroxystini, through a broad phylogenetic analysis of the subfamily Paederinae, reconstructing the most inclusive Paederinae phylogeny to date.

1.1. The state of phylogenetic research on Paederinae

The phylogenetic relationships of Paederinae at tribal and subtribal level are poorly studied. There have only been three phylogenies that cover the subfamily broad enough to address these, all recently published (Schomann and Solodovnikov, 2017; Żyła et al., 2019; Bogri et al., 2020). Surprisingly, despite the domination of molecular approaches in phylogenetic systematics over the last several decades, no focused molecular phylogenetic study of Paederinae was attempted until as late as 2017 (Schomann and Solodovnikov, 2017).

Earlier phylogenetic studies (e.g. Herman, 1981, 1991, 2010; Frania,

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1986a, b; Drugmand and Wauthy, 1992) were focused exclusively on morphological data. Moreover, these previous studies were too narrow in scope, as they focused on generic revisions of specific subtribes, thus not covering the entire subfamily. Some understanding of phylogenetic relationships of Paederinae resulted from broader molecular phylogenetic analyses focused on Scarabaeiformia and Staphyliniformia (McKenna et al., 2015, 11 Paederinae genera, two gene fragments).

All three phylogenetic studies covering Paederinae more broadly (Schomann and Solodovnikov, 2017; Żyła et al., 2019; Bogri et al., 2020) were limited in their taxon sampling of the subfamily. The first molecular phylogeny of Paederinae (Schomann and Solodovnikov, 2017) was based on five gene fragments, but the main target of that study was to find the phylogenetic placement of a single genus, *Hyperomma* Fauvel. Because of that specific goal, the study included only 17 genera that covered all subtribes of Pinophilini and Paederini, and six out of seven subtribes of Lathrobiini. With the aim to place some Burmese amber fossils in the Paederinae classification, Żyła et al. (2019) added two more gene fragments, five more genera and a morphological partition to that dataset and brought the first total-evidence analysis of Paederinae, combining molecular and morphological data. This study resulted in the largest molecular phylogeny of the subfamily, thus far, and the first containing a matrix of morphological characters for spanning the diversity of Paederinae. The latest phylogenetic effort was undertaken by Bogri et al. (2020), who significantly expanded the morphological matrix for Paederinae, especially with taxa and characters relevant to Lathrobiini, in order to find the systematic position of two Baltic amber fossils. Up to now, only 35 Paederinae genera had been included in any phylogenetic analysis. These genera represent three out of the four tribes of Paederinae, as the tribe Cylindroxystini has never been included in a subfamily-wide analysis. We document that and the increasing representation of Paederinae genera in phylogenetic analyses in the form of a timeline in Appendix A (File A.1).

All the previous phylogenetic studies agreed that Paederinae are a monophyletic group. The recently published molecular phylogeny by Żyła and Solodovnikov (2020) (15 Paederinae genera, seven gene fragments) shed more light on the sister-group relationship of the subfamily. Paederinae were resolved there as sister to the clade consisting of subfamilies Staphylininae, Xantholininae, Platyprosopinae and Coomaniinae. The same sister-group relationships for the monophyletic Paederinae were shown in Tihelka et al. (2020) who reanalyzed Żyła and Solodovnikov's (2020) dataset. Overall, the previous phylogenetic studies on Paederinae have made clear that more research is needed towards achieving a natural classification of this diverse and distinctive subfamily of rove beetles.

1.2. The taxonomic history of Paederinae tribes

As a result of this fundamental, yet limited, phylogenetic research on Paederinae, some changes in the tribal system were introduced. This has been particularly important because the taxonomic history of Paederinae has been rather complicated, with many groups used by convention without a rigorous examination of their monophyly, composition or sister-group relationships.

The history of the higher classification of Paederinae (see Schomann and Solodovnikov, 2017 for details) begins in the 19th century, with the erection of two separate but closely related groups (Nordmann, 1837; Erichson, 1839). The two groups, Paederini and Pinophilini, were then united to form the subfamily Paederinae by Ganglbauer (1895). Ganglbauer's system of Paederinae with these two tribes was followed by numerous European researchers but was only later adopted by their American counterparts (i.e., Casey, 1905; Blackwelder, 1939). In 1943, Bierig erected a monotypic tribe, Cylindroxystini, as the third tribe of Paederinae, which, however, was not mentioned again in the literature until Herman's revision (1991). In the meantime, Jeannel and Jarrige (1949) modified the tribal system of Paederinae to include three tribes, by dividing Paederini into Paederini and Lathrobiini. In 1991, Herman downgraded Bierig's (1943) neglected tribe, Cylindroxystini, to a subtribe, Cylindroxystina, and treated it as a member of the tribe Paederini (which included all non-Pinophilini Paederinae without recognizing Lathrobiini as a tribe). Thus, in the review of the Staphyliniformia classification and family-group nomenclature by Newton and Thayer (1992), Paederinae comprises only two tribes, Pinophilini and Paederini. This classification was followed until Schomann and Solodovnikov (2017) divided Paederini into Paderini and Lathrobiini, again. For practical reasons explained in detail in the next section, and without analysis, they raised the subtribe Cylindroxystina to the tribal level again, as Cylindroxystini. Therefore, currently Paederinae consists of four tribes, Pinophilini, Paederini, Cylindroxystini, and Lathrobiini.

Despite the progress in Paederinae classification, it has become evident from the three previous phylogenetic analyses (Schomann and Solodovnikov, 2017, Żyła et al., 2019; Bogri et al., 2020) that the sister group relationships between Pinophilini, Paederini and Lathrobiini are still uncertain. Besides that, the sister group relationships of the highly peculiar Neotropical tribe Cylindroxystini are completely unknown, as it has never been included in any phylogenetic analysis. Within the tribes, the biggest obstacle is that the classification of the most species-rich tribe – Lathrobiini, whose major subtribes Lathrobiina and Medonina are not monophyletic (Schomann and Solodovnikov, 2017; Żyła et al., 2019; Bogri et al., 2020) – has not yet been resolved.

1.3. Historical overview and challenges of the tribe Cylindroxystini

The taxonomic history of the tribe Cylindroxystini also begins in the 19th century, with the description of the genus *Neolindus* Scheerpeltz, to accommodate the single species *Neolindus religans* (Sharp), with the preoccupied name *Lindus* by Sharp (1876). Sharp placed the genus in the tribe Paederini (sensu Erichson, 1839) near *Lithocharis* Dejean (currently Lathrobiini). He did not explain what could support his view, but noted the similarity of *Neolindus* to *Oedichirus* Erichson (Pinophilini) and suggested that it might be a transitional form between the two tribes (Pinophilini and Paederini). Bierig (1943) erected a new tribe, Cylindroxystini, for his new species *Cylindroxystus longulus* Bierig which he also regarded as the link between the tribes Paederini and Pinophilini, but made no connection of his new tribe with *Neolindus*. Meanwhile, Blackwelder (1944), without giving any reasons, moved *Neolindus* to the subtribe Paederina. Fagel (1958) cited a few characters for *Neolindus*, but *N. religans* remained the only species in the genus for more than a century, until Irmler's work (1981) that added five more species.

Herman's (1991) work was a breakthrough in the study of Cylindroxystini. He was the first who placed *Cylindroxystus* Bierig and *Neolindus* together, adding 11 and 27 new species to them, respectively. He also downgraded Cylindroxystini to the subtribal level, Cylindroxystina, of the tribe Paederini in the broad sense (sensu Newton and Thayer, 1992), a subtribe including only these two genera. He provided a thorough diagnosis for the subtribe and each of the included genera, developed identification keys to the species, and discussed their intrageneric phylogenetic relationships. The reason that Herman (1991) reduced Cylindroxystini to a subtribe of Paederini was their small apical maxillary palpomere (palpomere 4), which was characteristic of the tribe Paederini (sensu Newton and Thayer, 1992). Since Herman's (1991) work, only six new species of *Neolindus* (Irmler, 2011; Asenjo, 2011; Assing, 2012) and one species of *Cylindroxystus* (Ramirez and Asenjo, 2017) were described, and currently, the genera comprise 39 and 15 species, respectively.

Schomann and Solodovnikov (2017) reinstated the tribal status of Cylindroxystina for practical reasons. Because of the lack of DNA-grade material, the group was not represented in their molecular phylogenetic analysis. Since the peculiar morphology of Cylindroxystina did not fit their Paederini or Lathrobiini, the group was treated as an easy-to-diagnose separate tribe, Cylindroxystini. The following phylogenetic analyses (Żyła et al., 2019; Bogri et al., 2020) did not investigate the status of Cylindroxystini, nor did they include any representatives in their taxon sampling.

In our study, we were able to sample DNA-grade material from both Cylindroxystini genera, thus motivating our phylogenetic analyses. We aim to resolve the phylogenetic position and systematic status of this enigmatic group, which has challenged rove beetle researchers for decades. To do so, we reconstruct the largest phylogeny for the subfamily Paederinae thus far.

2. Material and methods

2.1. Examination and deposition of taxa

For the morphological study, most of the recent specimens were boiled ca. 15 min. in 10% KOH, to soften and bleach them, which allowed for their dissection and better observation of exoskeletal structures. They were then rinsed in distilled water, disarticulated when necessary, and stored/examined in small Petri dishes with glycerine. Those taxa that were represented only by the specimen used for the DNA extraction, were studied without using KOH and kept in 95% ethanol.

All specimens used for the morphological matrix are kept at the Natural History Museum of Denmark in Copenhagen (NHMD, former ZMUC) unless indicated otherwise in Appendix B (Table B.1). Additional morphological observations on *Cylindroxystus* and *Neolindus* were made on-site without dissecting the specimens. Specimens used for these observations were deposited in the following institutions: AMNH, American Museum of Natural History, New York City, New York, USA (L. Herman); NMNH (former USNM), National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (late T. Erwin); SEMC, Snow Entomological Museum Collection, Biodiversity Institute, University of Kansas, Lawrence, Kansas, USA (Z. Fallin). Deposition of molecular vouchers is indicated in Appendix B (Table B.1).

The specimen of *Neolindus* was acquired during the field trip to Peruvian Amazon under the permit no RDG 0328-2017-SERFOR-DGGSPFFS/RDG 356-2017-SERFOR-DGGSPFFS.

2.2. Microscopy and illustrations

The specimens were examined using Leica M205 C and Leica M125 stereoscopes (Leica Microsystems GmbH, Wetzlar, Germany). Pictures were taken either with a Canon EOS 5D Mark III digital camera with a macro lens Canon MP-E 65 mm Ff2.8 1–5× using the remote shooting option of the Canon EOS Utility 3.4.30.0 software (Canon Inc., Ōta, Tokyo, Japan) or with a Leica M205A stereomicroscope with a Leica DM 6000 digital camera using a Leica Application Suite LAS 4.7.1 (Leica Microsystems, Wetzlar, Germany). Photomontage was accomplished using Zerene Stacker (Zerene Systems LLC, Richland, WA, USA) or using the Z-stacking option in LAS software. The photos were edited in Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, USA).

2.3. Taxon sampling and outgroup for phylogenetic analysis

In total, 76 taxa were included in the final combined dataset. Three of these taxa (*Scymbalium* Erichson, *Micrillus* Raffray, and *Scymbalopsis* Reitter) were represented in the morphological dataset only, as DNA-grade material was not available. We sampled all currently recognized subtribes of Paederinae and included both genera classified in the tribe Cylindroxystini. The combined dataset accounts for 57 Paederinae taxa (47 identified genera), of which 19 taxa have been sequenced *de novo*. Compared to the previous molecular studies, we doubled the number of genera included in the analysis, which results in the most extensive Paederinae taxon sampling so far. Since the gene sampling in Schomann and Solodovnikov (2017) did not include the 28S and CADA gene fragments, we extracted DNA from the same specimens, or the same taxa, and sequenced these missing loci. Compared to the previous studies using molecular data (Schomann and Solodovnikov, 2017; Żyła et al., 2019), the taxon sampling was most significantly expanded for the tribe Lathrobiini: 30 genera (28 identified and two not identified to genus level) included here with molecular data compared to eight and 13 Schomann and Solodovnikov (2017) and Żyła et al. (2019), respectively. We added representatives of closely related subfamilies, namely Staphylininae, Xantholininae, and Platyprosopinae (sensu Żyła and Solodovnikov, 2020) as the closer related outgroup, and representatives of Oxyporinae, Tachyporinae and Euaesthetinae were chosen as the more distantly related outgroup.

2.4. Morphological characters

The 123 morphological characters included in the present study were prepared with Mesquite v3.5 (Maddison and Maddison, 2018) and primarily derived from the matrices of Żyła et al. (2019) and Bogri et al. (2020) with more characters included. Unknown character states were coded with '?', while inapplicable states with '–'. The list of characters is provided as Appendix A (File A.2). The nexus file containing the character matrix is available as Appendix A (File A.3) and in MorphoBank (project no 3769; permalink: http://morphobank.org/permalink/?P3769).

2.5. DNA extraction, amplification, and sequencing

Whole genomic DNA was extracted non-destructively. The abdominal apex was removed from the specimens and used for the extraction (including segment VIII, the genital segment and, if male, the aedeagus). In the cases where the first extraction failed or the extract ran out, additional extractions were performed using other body parts, such as a leg, the pronotum, or even the whole specimen (if its size was minute). Following the extraction, the resulting physical voucher included the non-extracted portion of the specimen frozen in 96% ethanol and the extracted part, also frozen in 96% ethanol, in a separate vial. The vouchers of the extracted specimens are deposited in the Natural History Museum of Denmark (NHMD). The majority of the sequences were obtained following a previously used protocol for extraction and amplification (see Żyła et al., 2019 for the details). The rest of the sequences were obtained with the Qiagen DNeasy Blood and Tissue Kit (Qiagen Nordic, Copenhagen, Denmark) using the protocol for animal tissue (see Brunke et al., 2016 for the protocol). All extracts were stored in a −20 °C freezer, to avoid the fast fragmentation of DNA.

Seven gene fragments were selected for phylogenetic inference based on their performance at different taxonomic levels within Staphylinidae (Chatzimanolis, 2014; Brunke et al., 2016; Schomann and Solodovnikov, 2017; Chani-Posse et al., 2018) and in other Coleoptera (Wild and Maddison, 2008), and to make our study compatible with Schomann and Solodovnikov (2017) and Żyła et al., (2019). The genes are as follows: the nuclear protein-encoding genes carbamoylphosphate synthatase (CADA and CADC), topoisomerase I (TP), arginine kinase (ArgK), and wingless (Wg), the mitochondrial protein encoding cytochrome c oxidase I (COI), and the nuclear ribosomal 28S.

Polymerase chain reactions were performed in 25 μL reactions. Most of the sequences were amplified in the mastermix solution described in Żyła et al. (2019). For the rest of the sequences, the reaction consisted of 2 μL of DNA extract, 4 μL of 5x HOT FIREPol Blend Master Mix Ready to Load With 10 mM MgCl2 (Solis BioDyne, Tartu, Estonia), 0.5 μM of each primer and 15 μL of molecular grade water. In the case of the second reaction of the nested PCR, which was done for the amplification of CADA, TP, ArgK, and Wg, only 1 μL of DNA extract was used, with the analogous increase in molecular grade water, in both methods.

For amplification, we followed the process used by Żyła et al. (2019). Specifically, for amplification of 28S, TP, Wg and COI, we used the amplification profile from Chatzimanolis et al. (2010), whereas for ArgK the profile from Chatzimanolis (2014). In some cases, the amplification profiles of TP and Wg from Schomann and Solodovnikov (2017) were used. To amplify both CADA and CADC, we used Chatzimanolis (2014) protocol. Additionally, in some cases, to amplify CADA, we used the 'alternative profile' described by Brunke et al. (2016), while for CADC, we used an unpublished profile developed and kindly shared by A. Schomann: an initial denaturation at 96 °C for 7 min; 40 cycles of 96 °C for 30 s, 55 °C for 30 s and 72 °C for 1.5 min, and a final elongation step of 72 °C for 10 min. The annealing temperature of the amplification profiles was adjusted in certain cases of difficult amplifications. Before sequencing the samples, we assessed whether the PCR worked with gel-electrophoresis. In the cases of fade bands, the samples were put in the PCR-machine for 10–15 extra rounds, with the appropriate amplification profile. Complete primer details are given in Appendix B (Table B.2). Purification and sequencing were performed by Macrogen Europe B. V. (Amsterdam, Netherlands) in both directions.

2.6. Sequence assembly, management and alignment

Sequences were edited and assembled in Geneious v9.1.7 (Biomatters Ltd, Auckland, New Zealand) using De Novo Assembly with 'Highest Sensitivity/Slow' set and ends were trimmed with Error Probability Limit set from '0.005' to '0.05'. The GenBank accession numbers of all sequences are given in Appendix B (Table B.1). Sequences were aligned using the MAFFT plugin v1.3.6 in Geneious, based on MAFFT (Katoh et al., 2002). Protein-encoding genes were unambiguously aligned due to few gaps and their codon-based structure. 28S was aligned using the E-INS-i algorithm of MAFFT and ambiguously aligned regions were identified and removed with the server version of Gblocks (Talavera and Castresana, 2007). We allowed gap positions within the final blocks, and left the other settings as default. The resulting 28S alignment was 803 bp and had very few, scattered and usually single nucleotide gaps. Individual gene alignments were concatenated with the 'concatenate' function of Geneious. The concatenated sequence alignment is provided in Appendix A (File A.4) in nexus format.

2.7. Data matrix and partitioning

A combined matrix of molecular (4,631 bp) and morphological (123 characters) data for the total number of taxa under study (76) was analyzed using Bayesian inference. Gaps were treated as missing data in all analyses. Molecular and morphological data were also analyzed separately in order to account for differences in resolution between the two different datasets.

For the molecular data matrix, the alignment was initially partitioned by gene and, for protein-encoding genes, by codon position. The optimal partitioning scheme and the corresponding models of nucleotide evolution were determined by PartitionFinder v2.1.1 (Lanfear et al., 2016) using the Bayesian Information Criterion running on CIPRES Science Gateway v3.3 (http://www.phylo.org). All models were considered, branch lengths were unlinked and the search was set to the 'greedy' algorithm (Lanfear et al., 2012). The morphological data in the combined matrix were analyzed as a single, separate partition using the maximum likelihood model for discrete morphological character data, under the assumption that only characters that varied among taxa were included (Mkv) (Lewis, 2001). All analyses were performed using RevBayes v1.1.0 (Höhna et al., 2016) on the Iowa State University High Performance Computing (HPC) Condo Cluster.

2.8. Phylogenetic analysis in RevBayes

RevBayes is a program that provides a flexible framework for Bayesian phylogenetic inference. It gives a user the ability to design, specify, and implement new and complex phylogenetic models through the use of probabilistic graphical models and an interpreted programming language (Höhna et al., 2014, 2016). Our combined analysis integrates two separate likelihood components: one for molecular data and one for morphological data, to estimate the unrooted tree topology and associated model parameters (e.g., branch lengths, transition rates). We based our analyses on the following tutorials from the RevBayes website: https://revbayes.github.io/tutorials/ctmc/, https://revbayes.github.io/tutorials/fbd/fbd_specimen.html, and https://revbayes.github.io/tutorials/morph_tree/V2.html. Overall, we created three scripts containing all model parameters, moves, and functions, and a master Rev file that loads the data and the separate model files, and specifies the monitors and MCMC sampler (Appendix A, Files A.5–A.8). Scripts are also available at https://github.com/DagmaraZyla/Cylindroxystina_project.

For the tree model, we assumed a uniform distribution over topologies, where all possible labeled, unrooted trees have equal probability, and an exponential prior was applied to each of the branch lengths. The model component for the molecular data uses a general time-reversible model of nucleotide evolution, with gamma-distributed rate heterogeneity across sites and a proportion of invariant sites (GTR + I + G). We used flat Dirichlet prior distributions to describe uncertainty in stationary frequencies and exchangeability rates. In order to model gamma-distributed rates across sites, we applied an exponential prior on the shape parameter of the gamma distribution. We also specified a prior probability that a site is invariable using beta distribution. We assumed that all data subsets have independent substitution process parameters but share a common phylogeny (topology and branch lengths). The model component for the morphological data uses the Mkv model (Lewis, 2001) of morphological evolution. As in the molecular dataset, we allowed gamma-distributed rate heterogeneity among sites and we partitioned the dataset according to the number of character states. To correct for the ascertainment bias, we set coding to variable because we did not include invariant characters in our matrix (autapomorphies were included).

The combined analysis of morphological and molecular data was run for 200,000 generations, with an average of 361.3 moves/generation, and separate analyses of the molecular and morphological matrices for 100,000 generations, with an average of 361.3 and 256.3 moves/generation, respectively. All analyses included two independent runs.

We used Tracer v1.7 (Rambaut et al., 2018) to visualize and assess mixing of each MCMC run and diagnose convergence. The resulting 50% majority-rule consensus trees were examined in FigTree v1.4.4 (Rambaut and Drummond, 2016), and later edited and annotated in Adobe Illustrator CS6 (Adobe Systems, San Jose, CA, USA). Nodes with (BI) posterior probability (PP) > 0.95 were considered strongly supported; with PP $= 0.90$–0.94 moderately supported, and with PP $= 0.80$–0.89 weakly supported. Nodes with PP < 0.80 were considered to be unsupported.

3. Results

3.1. Phylogenetic analyses

PartitionFinder found the following four partitions: 1) ArgK3 + Wg1 + Wg3 + Wg2; 2) 28S + ArgK1 + TP1 + CADC1 + CADA1 + COI1 + TP2 + CADA2 + CADC2 + ArgK2 + COI2; 3) COI3; 4) TP3 + CADA3 + CADC3. For all but partition 3, GTR + I + G was found to be the best supported model. We additionally moved 28S to a separate partition as this is the only non-protein coding gene in our dataset. The third codon positions of COI were excluded as it has been suggested that they suffer saturation for deep divergences, which can potentially bias phylogenetic analyses (e.g., Swofford et al., 1996; Lin and Danforth, 2004). Since COI3 was excluded, all partitions were analyzed under GTR + I + G model.

Our independent Markov chains converged on the same stationary distribution as visualized in Tracer v1.7. Both combined and individual traces were inspected. The effective sample size (ESS) values were greater than 200 for all parameters indicating good mixing of the chains. The tree topology presented in Fig. 1 is the 50% majority-rule consensus tree. Clades of outgroup taxa were collapsed, but the full tree is provided as Appendix C (Fig. C.1).

The subfamily Paederinae was recovered as monophyletic with

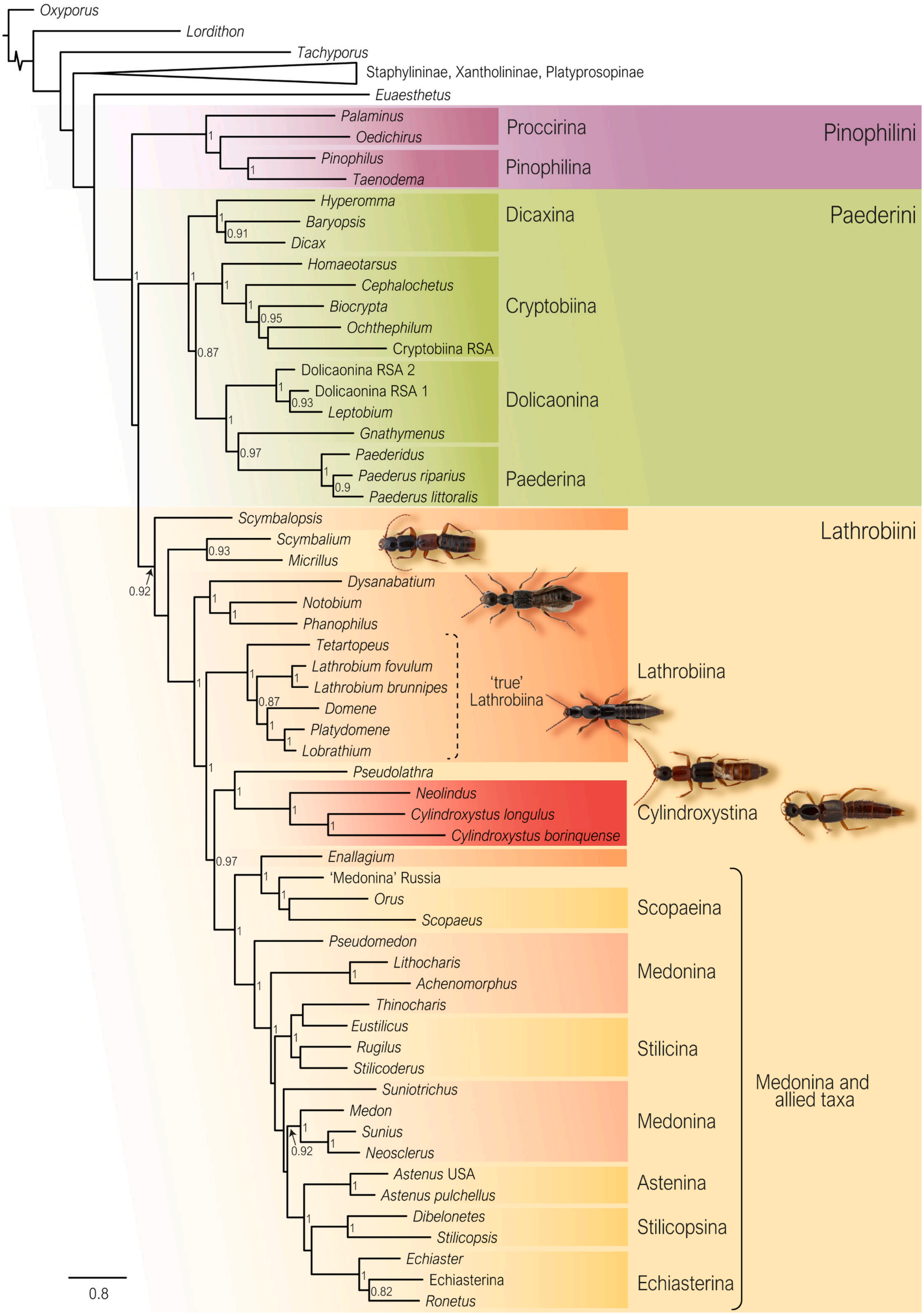

Fig. 1. Fifty per cent majority rule consensus tree from the Bayesian analysis of combined datasets. Posterior probabilities >80 are shown next to the corresponding nodes. Outgroups were collapsed. Habitus photos (from the top): *Scymbalium* sp., *Dysanabatium* sp., *Lathrobium* sp., *Pseudolathra* sp., and *Cylindroxystus* sp. Photo of *Lathrobium* by A.K. Hansen.

strong support, with a posterior probability equal to one (PP = 1). The tribes Pinophilini and Paederini were monophyletic with strong support (PP = 1 in both cases). The tribe Cylindroxystini was monophyletic (PP = 1), but was resolved nested within the tribe Lathrobiini, rendering Lathrobiini paraphyletic. This clade, containing Cylindroxystini and Lathrobiini, was moderately supported as monophyletic (PP = 0.92).

Within the tribe Pinophilini, the subtribe Pinophilina was resolved as monophyletic and strongly supported (PP = 1), while the subtribe Procirrina was not monophyletic.

Within the tribe Paederini, the subtribes Dicaxina, Cryptobiina and Paederina were recovered as monophyletic (PP = 1 in all cases). On the contrary, Dolicaonina was not monophyletic, with the genus *Gnathymenus* resolved as sister to Paederina (PP = 0.97). The rest of Dolicaonina taxa were resolved together in one strongly supported clade (PP = 1).

Within the tribe Lathrobiini, several subtribes were found to be non-monophyletic. The genus *Scymbalopsis*, currently in Lathrobiina, was estimated to be sister to all the other taxa. The first clade that branched off was moderately supported and contained the genera *Micrillus* and *Scymbalium*, both currently Lathrobiini *insertae sedis* (Bogri et al. 2020). The second clade to branch off was well-supported (PP = 1), sister to the rest of Lathrobiini (PP = 1), and consisted of *Dysanabatium* Bernhauer (PP = 1) sister to *Notobium* Solsky + *Phanophilus* Sharp (PP = 1), all three genera currently classified in Lathrobiina. The next clade was resolved sister to the remaining Lathrobiini (PP = 1), and comprised six Lathrobiina taxa (PP = 1) from five genera.

The next to branch off was a well-supported clade (PP = 1), consisting of *Pseudolathra* Casey (Lathrobiina) sister to the monophyletic (PP = 1) tribe Cylindroxystini (PP = 1). This clade was resolved as sister (P = 0.97) to the strongly supported 'Medonina and allied taxa' clade (PP = 1).

Within the 'Medonina and allied taxa' clade, the clade consisting of *Enallagium* Bernhauer (Lathrobiina) and Scopaeina branched off first with strong support (PP = 1) and was recovered sister to the remaining Lathrobiini (PP = 1). The subtribe Medonina was recovered as not monophyletic, with most of its genera forming two separate but well supported clades (both PP = 1). The subtribe Stilicina was recovered together with *Thinocharis* Kraatz (Medonina) as a strongly supported clade (PP = 1). The subtribes Astenina + (Stilicopsina + Echiasterina) were estimated as monophyletic, forming one well supported clade (PP = 1).

The tree resulting from the molecular analysis (Appendix C, Fig. C.2.A) was almost identical in its topology with the total-evidence tree. The overall results of the separate analysis of morphological data were rather congruent with the result of the molecular and combined analyses at the shallower level, but with a lower resolution at the tribal and subtribal level. There were also differences in the resolution at the shallower level among some clades (resulting tree is shown in Appendix C, Fig. C.2.B). One of the main differences was that the tribe Lathrobiini was not resolved as monophyletic and 'Medonina and allied taxa' were

Fig. 2. Morphology of Cylindroxystina. A. Head of *Cylindroxystus* sp., dorsal view; B. Head of *Neolindus* sp., ventral view; C. Part of the abdomen of *Cylindroxystus* sp., lateral view. Abbreviations: m - mandibula; mp - maxillary palpomere; gs - gular sutures; pt - paratergite.

especially poorly resolved. Among Lathrobiini, the genera *Dysanabatium*, *Notobium* and *Phanophilus* were not resolved together. The monophyly and the position of Cylindroxystini as sister to the genus *Pseudolathra* within the Lathrobiini (or part of Lathrobiini in the morphology-only analysis) was consistently recovered in all analyses.

3.2. Systematics

Order Coleoptera Linnaeus, 1758
Family Staphylinidae Latreille, 1802
Subfamily Paederinae Fleming, 1821
Tribe Lathrobiini Laporte, 1835
Subtribe Cylindroxystina Bierig, 1943 status reinstated
Type genus: *Cylindroxystus* Bierig, 1943
Genera included: *Cylindroxystus*, *Neolindus* Scheerpeltz, 1933

Diagnosis: apical maxillary palpomere (palpomere 4) nipple-shaped (Fig. 2A), mandibles falcate and edentate (Fig. 2A), gular sutures far from each other (Fig. 2B), abdomen with a pair of paratergites on segment III only (Fig. 2C), segments IVVII without paratergites.

Notes: Both *Cylindroxystus* and *Neolindus* have been collected remarkably rarely and in small numbers; numerous species are represented only by single specimens. The revision by Herman (1991) is based on a total of merely 37 *Cylindroxystus* specimens and 79 *Neolindus* specimens. However, a recent collection visit to the Kansas University Biodiversity Institute by the first author (DŻ) revealed over 200 additional specimens of both genera with several new country records and new species (Żyła, in prep.).

4. Discussion

Using a multilocus dataset combined with morphological data, and a taxon sample far more comprehensive than the other phylogenies of Paederinae (Schomann and Solodovnikov, 2017; Żyła et al., 2019; Bogri et al., 2020), we show strong support for the monophyly and sister group relationships of Cylindroxystini. Simultaneously, we provide the largest phylogeny estimated for this subfamily to date. For the first time, all currently recognized tribes of Paederinae were included in an analysis of both molecular and morphological data. This allows us to make some decisions concerning the classification and future directions in the research of this subfamily.

4.1. Phylogenetic position of genera Cylindroxystus and Neolindus

This is the first time that the tribe Cylindroxystini was included in a phylogenetic analysis across Paederinae, and our estimates support its placement as a lineage nested within a clade of taxa currently in Lathrobiini. These findings illuminate the sister-group relationships of this morphologically derived group and show that Cylindroxistini should be downgraded again to a subtribe within the tribe Lathrobiini. Characters supporting the placement of the group within Lathrobiini are the gular sutures that become indistinct and do not reach the posterior margin of the head, the postoccipital suture crossing the gular sutures, the presence of a transversal carina in the furcasternum of prosternum, the presence of two different surfaces on the metacoxa and the lack of anteromedian gland.

Cylindroxystina *status reinstated* was resolved as sister to the genus *Pseudolathra*, a result that was not suspected before and thus surprising at first. However, careful evaluation of the morphological characters revealed significant similarities between all three genera hidden under striking derived features of Cylindroxystina (Fig. 3A–C). These shared characters are as follows: body glossy, apical maxillary palpomere (palpomere 4) small, nipple-like or conical; gular sutures widely separated; protibial combs arranged diagonally; punctures on elytra in distinctive rows; additional ridge on epipleuron (absent in some modified *Pseudolathra,* e.g. from Oceania); aedeagus with additional sclerites, highly modified (fewer sclerites in *Cylindroxystus*). Nevertheless, we decided to not include *Pseudolathra* into Cylindroxystina. We made that decision because both *Cylindroxystus* and *Neolindus* are distinctive, highly derived, and geographically restricted genera that make an easily diagnosable clade. Adding the widespread and less modified *Pseudolathra* would weaken the diagnosis of the group.

Furthermore, such a move would be premature, as we rather believe that we found a sister clade to Cylindroxystina where *Pseudolathra* is just one of the genera making this clade. Based on the shared characters revealed for the *Pseudolathra*-Cylindroxystina clade, and biogeographic considerations, we anticipate that *Dacnochilus* LeConte and *Paederopsis*

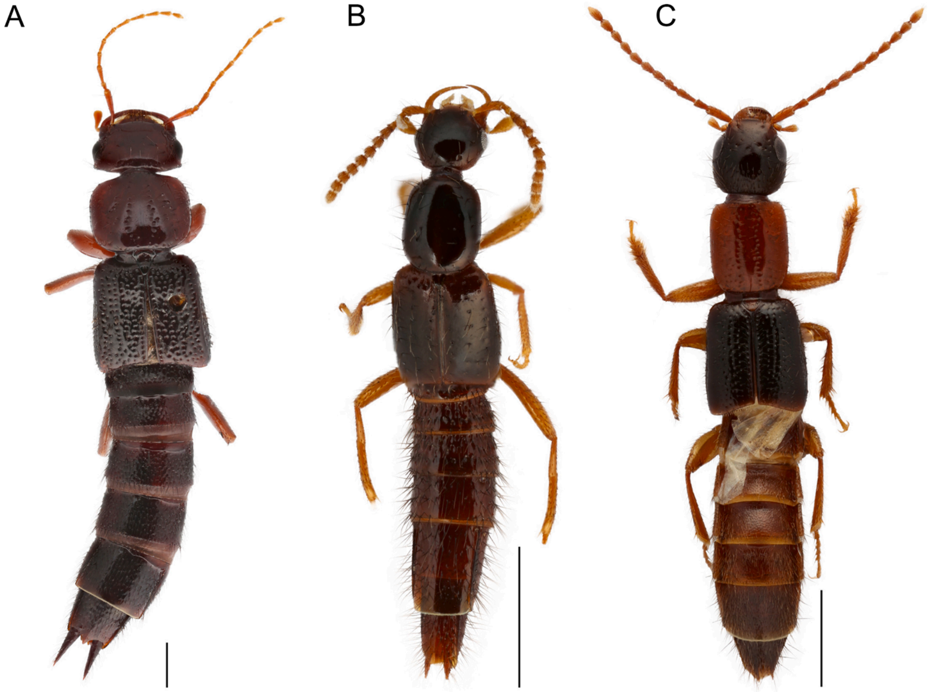

Fig. 3. Habitus of representatives of *Pseudolathra*-Cylindroxystina lineage. A. *Neolindus* sp.; B. *Cylindroxystus* sp.; C. *Pseudolathra* sp. Scale bars represent 1 mm.

Wasman are at least two other genera that may be a part of this suspected new lineage. More research on these and other genera of Paederinae is needed to reveal what is the composition of this lineage. Currently, based on our analysis, we only remove *Pseudolathra* from Lathrobiina and place it as Lathrobiini *incertae sedis*.

4.2. Geographical distribution of Cylindroxystina and Pseudolathra

As mentioned before, both genera of Cylindroxystina occur exclusively in the Neotropical ecozone (as defined by Schultz, 2005) and have almost overlapping distribution, except for the Caribbean region (*Cylindroxystus* only), French Guiana, Suriname, Bolivia, and South Mexico (*Neolindus* only) (Fig. 4). The distribution of the sister genus, *Pseudolathra* spans across all continents except for Antarctica and Australia, with more species living in subtropical and tropical regions, especially in Indomalayan and Nearctic realms (38 and 33, respectively) (Fig. 4). The absence of published records of this genus in Australia is an artefact of the poor knowledge of the rove beetle fauna and systematics of that continent. We are aware of specimens from Australia which fit the current concept of the genus *Pseudolathra* (AS, personal observation). So far, there are no described fossils of the *Pseudolathra*-Cylindroxystina lineage, but we are aware of at least one amber inclusion in Baltic amber. Based on the current distribution and relative species richness, we hypothesize that the lineage could have originated in Asia and dispersed to Europe and then to North America at the beginning of the Paleocene–Eocene Thermal Maximum (PETM), ca. 55.5 Ma (Sanmartin et al., 2001; Storey et al., 2007). Such scenario suggests that, unlike *Pseudolathra*, the crown Cylidroxystina is a relatively young clade which underwent rapid diversification in South America, which could have been a result of the Great American Biotic Interchange starting in the late Miocene (Rull, 2020). It is noteworthy that *Dacnochilus* and *Paederopsis,* both putative members of the *Pseudolathra*-Cylindroxystina lineage, are confined to North and South America and absent on other continents. Such a hypothetical younger age of Cylindroxystina would be consistent with the main result of our study that changes the view of them as an isolated group within Paederinae to a lineage nested within Lathrobiini.

4.3. Comparison of our phylogeny with the previous Paederinae phylogenies

The overall tree topology was consistent with the previous analyses by Schomann and Solodovnikov (2017), Żyła et al. (2019) and Bogri et al. (2020). As in all three previous studies, our analyses also recovered Paederinae as monophyletic.

Our total-evidence analysis resolved the sister-group relationships between the tribes, in agreement with the analogous analysis of Żyła et al. (2019) and the morphological analysis in Bogri et al. (2020), providing strong evidence that Pinophilini are sister to Paederini + Lathrobiini. For the first time, the subtribes Pinophilina and Procirrina are represented by more than one species per subtribe, and Pinophilina was revealed as monophyletic. All the subtribes within Paederini were recovered as monophyletic, in congruence with previous studies, except for Dolicaonina whose genus *Gnathymenus* was estimated as sister to Paederina. This genus, known exclusively from North and South America, was originally described in the subfamily Oxytelinae (Solier, 1849), but was later transferred to Paederinae and considered to be related to *Paederus Fabricius* (e.g. Kraatz, 1857; Fairmaire and Germain, 1861). This relationship to *Paederus* was followed by almost all subsequent authors until Herman (1981) formally transferred it into Dolicaonina in his revision without explicit justification. Our result suggests that *Gnathymenus* belongs, in fact, to the subtribe Paederina, but more dense taxon sampling of both subtribes would be needed to make a formal decision. Regarding the phylogenetic relationships between the Paederini subtribes, our analysis agrees with Żyła et al. (2019), and thus does not agree with the results of Schomann and Solodovnikov (2017) and Bogri et al. (2020). More detailed questions regarding the sister group relationships within Paederini should be addressed with the

Fig. 4. Geographical distribution of representatives of *Pseudolathra*-Cylindroxystina lineage. *Pseudolathra* range inferred from Newton A., unpublished database, and personal observation (AS); Cylindroxystina range inferred from Newton A., unpublished database, literature, and personal observation (DŻ).

inclusion of more taxa from the subtribes in a future analysis.

Regarding Lathrobiini, our analyses are largely congruent with the previous studies. The subtribe Lathrobiina was once again confirmed as non-monophyletic. The genera *Micrillus* and *Scymbalium* were recovered as sister to the rest of Lathrobiini, clearly outside Lathrobiina, in agreement with Bogri et al. (2020). The clade with *Notobium*, *Phanophilus* and *Dysanabatium* was also resolved outside Lathrobiina, as was suggested in the previous papers, taking into account that the taxon that Schomann and Solodovnikov (2017) and Żyła et al. (2019) refer to as *Scymbalium* is in fact a *Notobium*. *Pseudolathra* here was resolved in a very different place compared to the results in Bogri et al. (2020), as sister to Cylindroxistini. That study, however, did not include any representative of Cylindroxistini and was based on morphological data only. The placement of the remaining Lathrobiina genera was congruent among studies. The subtribe Medonina was also confirmed as non-monophyletic, as already suggested by Żyła et al. (2019) and Bogri et al. (2020), despite local differences in the tree topology among the studies.

4.4. Paraphyly of Lathrobiina and the 'true' Lathrobiina

The subtribe Lathrobiina (ca. 1,400 species), in the current sense, was not monophyletic in our resulting phylogeny. *Scymbalopsis*, which was resolved as sister to all other Lathrobiini, is a small and enigmatic genus known only from the mountains of Central and Western Asia (Shavrin and Anichtchenko, 2019; Newton A., unpublished database). This is the first time where the genus has been included in a phylogenetic study, although with morphological data only. Our results indicate its isolated phylogenetic position and its exclusion from the subtribe Lathrobiina. *Micrillus* and *Scymbalium* clearly form one separate lineage. These two genera were already resolved together and outside Lathrobiina in Bogri et al. (2020), therefore our results support their recent change of classification as Lathrobiini *insertae sedis*. We hypothesize that they are, in fact, a separate subtribe, but we are not making the formal taxonomic decision yet because of the lack of molecular material from this lineage and the limited taxon sampling.

The genera *Notobium*, *Phanophilus* and *Dysanabatium* form another separate lineage. This lineage can be distinguished from the *Micrillus-Scymbalium* lineage by their soft mesothorasic membrane without sclerotized areas, the parallel sterno-pleural sutures and the double lateral ridges of the mesosternum, the bilobed protarsomere 4, and metatarsomere 1 being shorter than metatarsomere 5. Furthermore, the *Notobium-Phanophilus-Dysanabatium* lineage can be distinguished from the rest of Lathrobiina by its elongated regular penultimate maxillary palpomere (palpomere 3), the lack of widened projection supporting the protibial comb-like rows of setae (protibial combs), the numerous protibial combs (more than ten), and mesotarsomere 1 being longer than mesotarsomere 2. Additional research should be done to identify more members of this lineage.

In our analysis, the 'true' Lathrobiina clade was formed by five genera, namely: *Domene* Fauvel, *Lathrobium* Gravenhorst, *Lobrathium* Mulsant & Rey, *Platydomene* Ganglbauer and *Tetartopeus* Czwalina. The most important synapomorphic character for the diagnosis of this lineage is the expanded area of the protibia that holds the comb-like rows of setae (protibial combs). Among the taxa studied here, the only other genus from Lathrobiini with such protibia expansion is *Scymbalopsis*. However, the pattern of the combs in *Scymbalopsis* is different suggesting that this similarity with *Lathrobium* and allies is convergent. In addition to the comb-like row of setae, the 'true' Lathrobiina clade presents consistently a combination of other characters such as tomentose pubescence on antennomere 3, vase-like shaped penultimate maxillary palpomere (palpomere 3), transversal carina between sterno-pleural sutures of mesosternum pointed towards abdomen, meso- and metatarsomere 1 shorter than meso- and metatarsomere 2, and finally metatarsomere 5 very long (equal or longer than metatarsomeres 2–4 combined). Future research would restrict the composition of Lathrobiina and provide much-needed changes in the classification of Paederinae.

4.5. Challenges within 'Medonina and allied taxa'

The remaining subtribes of Lathrobiini, referred to as 'Medonina and allied taxa', form a well-supported clade that is distinguished from the rest of Lathrobiini by the small and acicular last maxillary palpomere (palpomere 4) and the presence of apical ctenidium on the one side of metatibia only. The lineage currently consists of six subtribes, namely Medonina, Astenina, Stilicina, Stilicopsina, Echiasterina and Scopaeina, all together accounting for around 3,000 described species. According to our results, the rank and the composition of the subtribes do not reflect the phylogenetic relationships but rather are based on likely convergent morphological similarities. The most complicated situation concerns the subtribe Medonina, and in our phylogeny, the majority of its genera were placed in two independent clades, each without a clear diagnosis for the moment. These new lineages should be researched in the future to define their morphological characters. The subtribe Scopaeina was recovered as monophyletic and sister to *Enallagium*, a morphologically interesting genus currently placed in Lathrobiina, which bears a mixture of characters from both 'true' Lathrobiina and 'Medonina and allied taxa' lineages. The three included genera of the subtribe Stilicina were also recovered together, but in a clade with *Thinocharis* from Laos, currently a member of Medonina. All these show how far we are from the natural classification of this clade, especially the most species-rich subtribe Medonina. Such problem is partly a result of treating the subtribe as the so-called 'trash can' group meaning that any new species that did not clearly belong to any other group, was placed in Medonina resulting in a poly- or paraphyletic group now, without a clear definition and taxonomic boundaries. More phylogenetic effort and further reclassification would help with this issue.

5. Conclusions

The most important outcome of this study is the resolution of the systematic position and sister group relationships of the former tribe Cylindroxystini. Following that, we re-established the subtribal status of the group, now Cylindroxystina *status reinstated*. Building upon previous phylogenetic analyses on Paederinae, we significantly expanded the taxon sampling, including 18 genera that had never been analyzed before. This increased our understanding of the phylogenetic relationships within the subfamily. We confirmed the non-monophyletic nature of Lathrobiina and identified characters for the future separation of the 'true' Lathrobiina from the two other lineages traditionally placed in the subtribe. We also confirmed the non-monophyly of Medonina and enhanced the resolution of the systematically challenging 'Medonina and allied taxa' group. In our opinion, further expansion of taxon sampling to include more generic diversity and more species from different biogeographic regions, and also from hyperdiverse but unrevised genera, will help to further resolve phylogenetic questions on the subfamily and aid the revision of its classification at all levels.

CRediT authorship contribution statement

Dagmara Żyła: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Supervision. **Amalia Bogri:** Conceptualization, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Tracy A. Heath:** Resources, Writing - review & editing. **Alexey Solodovnikov:** Resources, Writing - review & editing.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2020.107059.

References

Asenjo, A., 2011. First record of *Neolindus* Scheerpeltz from French Guiana (Coleoptera, Staphylinidae, Paederinae), with a key to males. ZooKeys 135, 57–67.

Assing, V., 2012. Two new species of *Neolindus* from Peru and Venezuela (Coleoptera: Staphylinidae: Paederinae: Cylindroxystina). Beiträge zur Entomologie = Contributi. Entomol. 62 (2), 291–297.

Bierig, A., 1943. Algunos estaphylinidae (Col.) nuevos de Costa Rica. Rev. Chil. Hist. Nat. 45, 154–163.

Blackwelder, R.E., 1939. A generic revision of the staphylinid beetles of the tribe Paederini. Proc. U.S. Natl. Mus. 87 (3069), 93–125.

Blackwelder, R.E., 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part I. United States National Museum Bull. 185 xii + 1–188.

Bogri, A., Solodovnikov, A., Kypke, J.L., Żyła, D., 2020. Baltic amber members of the extant *Micrillus-Scymbalium* lineage of the Paederinae rove beetles (Coleoptera, Staphylinidae) and their systematic and ecological significance. Invertebrate System. 34 (5), 451–473.

Brunke, A.J., Chatzimanolis, S., Schillhammer, H., Solodovnikov, A., 2016. Early evolution of the hyperdiverse rove beetle tribe Staphylinini (Coleoptera: Staphylinidae: Staphylininae) and a revision of its higher classification. Cladistics 32, 427–451.

Casey, T.L., 1905. A revision of the American Paederini. Trans. Acad. Sci. St Louis XV (2), 17–248.

Chani-Posse, M., Brunke, A.J., Chatzimanolis, S., Schillhammer, H., Solodovnikov, A., 2018. Phylogeny of the hyper-diverse rove beetle subtribe Philonthina with implications for classification of the tribe Staphylinini (Coleoptera: Staphylinidae). Cladistics 34, 1–40.

Chatzimanolis, S., 2014. Phylogeny of xanthopygine rove beetles (Coleoptera) based on six molecular loci. Syst. Entomol. 39, 141–149.

Chatzimanolis, S., Cohen, I.M., Schomann, A., Solodovnikov, A., 2010. Molecular phylogeny of the mega-diverse rove beetle tribe Staphylinini (Insecta, Coleoptera, Staphylinidae). Zoolog. Scr. 39, 436–449.

Drugmand, D., Wauthy, G., 1992. Eléments de morphologie des Cryptobiina afropicaux (Coleoptera Staphylinidae Paederinae). Bulletin de l'Institut royal de Sciences naturelles de Belgique, Entomologie 62, 5–31.

Erichson, W.F., 1839. Genera et Species Staphylinorum Insectorum Coleopterorum Familiae, pt. 1. F. H. Morin, Berlin, Germany.

Fagel, G., 1958. Paederini (Coleoptera Polyphaga) fam. Staphylinidae. Exploration du Parc National Upemba Mission de Witte 1946–1949. Brussels 51, 1–470.

Fairmaire, M.L., Germain, P., 1861. Revision des Coléoptères du Chili (Suite 1). Annales de la Société Entomologique de France 4 (1), 404–457.

Frania, H.E., 1986a. Larvae of *Eustilicus* Sharp, *Deroderus* Sharp, *Stilocharis* Sharp, and *Medon* Stephens (Coleoptera: Staphylinidae: Paederinae: Paederini), and their phylogenetic significance. Can. J. Zool. 64, 2543–2557.

Frania, H.E., 1986b. Status of *Eustilicus* Sharp, *Trochoderus* Sharp, *Deroderus* Sharp, and *Stilocharis* Sharp (Coleoptera: Staphylinidae: Paederinae: Paederini) with implications for classification of the Medonina and Stilicina. Can. J. Zool. 64, 467–480.

Ganglbauer, L., 1895. Die Käfer von Mitteleuropa. II. Band. Familienreihe Staphylinoidea, 1. Teil: Staphylinidae, Pselaphidae. Carl Gerold's Sohn, Vienna, Austria.

Herman, L.H., 1981. Revision of the subtribe Dolicaonina of the New World, with discussions of phylogeny and the Old World genera (Staphylinidae, Paederinae). Bull. Am. Museum Natural History 167, 331–520.

Herman, L.H., 1991. Revision of the subtribe Cylindroxystina (Coleoptera: Staphylinidae: Paederinae). Bull. Am. Museum Natural History 203, 1–83.

Herman, L.H., 2010. Generic revision of the Procirrina (Coleoptera, Staphylinidae, Paederinae, Pinophilini). Bull. Am. Museum Natural History 347, 1–78.

Höhna, S., Heath, T.A., Boussau, B., Landis, M.J., Ronquist, F., Huelsenbeck, J.P., 2014. Probabilistic graphical model representation in phylogenetics. Syst. Biol. 63, 753–771.

Höhna, S., Landis, M.J., Heath, T.A., Boussau, B., Lartillot, N., Moore, B.R., Huelsenbeck, J.P., Ronquist, F., 2016. RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. Syst. Biol. 65, 726–736.

Irmler, U., 1981. Neue Arten der neotropischen Gattung Neolindus Scheerpeltz (Coleoptera, Staphylinidae). Stud. Neotropical Fauna Environ. 16, 209–215.

Irmler, U., 2011. Two new species and a new record of the genus *Neolindus* Scheerpeltz, 1933 (Coleoptera: Staphylinidae: Paederinae). Bonn Zoolog. Bull. 60 (1), 103–107.

Jeannel, R., Jarrige, J., 1949. Biospeologica, LXVIII. Coléoptères Staphylinides (Première Série). Arch. Zoologie Expérimentale et Générale 86, 255–392.

Katoh, K., Misawa, K., Kuma, K.I., Miyata, T., 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res. 30 (14), 3059–3066.

Kraatz, G., 1857. Naturgeschichte der Insekten Deutschlands. Abt. 1. Coleoptera, vol. 2, Nicolai, Berlin, Germany, pp. 377–768.

Lanfear, R., Calcott, B., Ho, S.Y., Guindon, S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29, 1695–1701.

Lanfear, R., Fransen, P.B., Wright, A.M., Senfeld, T., Calcott, B., 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol. Biol. Evol. 34, 772–773.

Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Syst. Biol. 50, 913–925.

Lin, C.P., Danforth, B.N., 2004. How do insect nuclear and mitochondrial gene substitution patterns differ? Insights from Bayesian analyses of combined datasets. Mol. Phylogenet. Evol. 30, 686–702.

Maddison, W.P., Maddison, D.R., 2018. Mesquite: A Modular System for Evolutionary Analysis. URL: http://mesquiteproject.org.

McKenna, D.D., Farrell, B.D., Caterino, M.S., Farnum, C.W., Hawks, D.C., Maddison, D. R., Seago, A.E., Short, A.E.Z., Newton, A.F., Thayer, M.K., 2015. Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. Syst. Entomol. 40 (1), 35–60.

Newton, A.F., Thayer, M.K., 1992. Current Classification and Family-Group Names in Staphyliniformia (Coleoptera). Fieldiana: Zoology (New Series) 67, 1–92.

Nordmann, A., 1837. Symbolae ad monographiam staphylinorum. Typis Academiae Caesareae Scientiarum, Commentariorum 4, 1–167.

Rambaut, A., Drummond, A.J., 2016. FigTree v1. 4.4. Institute of Evolutionary Biology, University of Edinburgh. Accessed from https://github.com/rambaut/figtree/releases.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst. Biol. 67 (5), 901.

Ramirez, J., Asenjo, A., 2017. First record and a new species of Cylindroxystus Bierig (Coleoptera, Staphylinidae, Paederinae) in Colombia. Zootaxa 4341 (3), 437–440.

Rull, V., 2020. Neotropical diversification: historical overview and conceptual insights. In: Rull, V., Carnaval, A.C. (Eds.), Neotropical Diversification: Patterns and Processes. Springer, Switzerland, pp. 13–49.

Sanmartin, I., Enghoff, H., Ronquist, F., 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biol. J. Linn. Soc. 73 (4), 345–390.

Schomann, A., Solodovnikov, A., 2017. Phylogenetic placement of the austral rove beetle genus *Hyperomma* triggers changes in classification of Paederinae (Coleoptera: Staphylinidae). Zoolog. Scr. 46, 336–347.

Schultz, J., 2005. The Ecozones of the World: The Ecological Divisions of the Geosphere. Springer, Berlin, Germany.

Sharp, D., 1876. Contributions to an insect fauna of the Amazon Valley. Coleoptera-Staphylinidae. Trans. Entomolog. Soc. London 1876, 27–424.

Shavrin, A., Anichtchenko, A., 2019. A new species and a new record of the genus Scymbalopsis (Coleoptera: Staphylinidae: Paederinae: Paederini). Acta Entomologica Musei Nationalis Pragae 59 (1), 185–188.

Solier, A.J.J., 1849. Zoologia. Tomo Cuarto. Insectos. Orden III. Coleopteros. [pp. 105–380, 414–511, pls. 1–12]. In: Gay, C. (Ed.), Historia fisica y politica de Chile, Paris, France, pp. 511.

Storey, M., Duncan, R.A., Swisher, C.C., 2007. Paleocene-Eocene thermal maximum and the opening of the northeast Atlantic. Science 316, 587–589.

Swofford, D.L., Olsen, G.J., Waddell, P.J., Hillis, D.M., 1996. Phylogenetic inferences. In: Hillis, D.M., Moritz, C., Mable, B.K. (Eds.), Molecular Systematics, 2nd ed. Sinauer, Sunderland, Massachusetts, USA, pp. 407–514.

Talavera, G., Castresana, J., 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst. Biol. 56, 564–577.

Tihelka, E., Thayer, M.K., Newton, A.F., Cai, C., 2020. New Data, Old Story: Molecular Data Illuminate the Tribal Relationships among Rove Beetles of the Subfamily Staphylininae (Coleoptera: Staphylinidae). Insects 11 (3), 164.

Wild, A.L., Maddison, D.R., 2008. Evaluating nuclear protein-coding genes for phylogenetic utility in beetles. Mol. Phylogenet. Evol. 48, 877–891.

Żyła, D., Yamamoto, S., Jenkins Shaw, J., 2019. Total-evidence approach reveals an extinct lineage of Paederinae rove beetles from Cretaceous Burmese amber. Palaeontology 62 (6), 935–949.

Żyła, D., Solodovnikov, A., 2020. Multilocus phylogeny defines a new classification of Staphylininae (Coleoptera, Staphylinidae), a rove beetle group with high lineage diversity. Syst. Entomol. 45 (1), 114–127.